MALE BEHAVIOR AND FEMALE RECRUITMENT IN THE RED-WINGED BLACKBIRD

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In most species of birds females devote more energy to reproduction than do males. Consequently natural selection has favored increased discrimination on the part of the females when seeking a mate and thus, in such species, selection of mates is expected to be determined by female choice (Trivers 1972). This would be particularly true in highly polygynous species where the male role in reproduction is very limited. The factors on which female choice can be based are individual differences among males and differences among the territories of males (Orians 1969). When the male contribution to reproduction is restricted to supplying genetic information, or when pair bonds are made away from breeding grounds, female choice must rely solely on differences in individual characteristics (Verner 1964). However, as the male contribution increases to include the maintenance of a territory which influences reproductive success through provision of food or nest sites, then female choice should also be influenced by territory quality (Orians 1969). This latter point has formed the basis for the Orians-Verner model for the evolution of polygynous mating systems (Selander 1972, Wilson 1975).

The Orians-Verner model attributes polygynous mating to the existence of major differences in territory qualities. When these differences are great enough, a female will improve her chances of successfully reproducing by choosing to share a high quality territory with another female rather than by choosing to be the sole female in a poor quality territory. Implicit in this model is that the differences in males' individual characteristics will be reflected by differences in the qualities of their territories, since the fittest males should be best able to defend superior territories. It follows then that female choice will be meditated by territory quality and therefore behavioral differences in males should not influence female recruitment. One might further predict that selection would favor a reduction in recruitment and courtship behavior since it should lack any advantage in attracting mates while making the male more vulnerable to predators.

From a study of Red-winged Blackbirds (*Agelaius phoeniceus*) we have shown that female choice as reflected by harem size, did not correlate with territory quality (Weatherhead and Robertson 1977). Some females therefore appeared to be making poor choices in terms of territory quality. We concluded that these choices must result from behavioral influences of territorial males not associated with the quality of their territories. Although

such choices lower reproductive success in the F_1 generation, we developed a model which showed that as long as those losses did not exceed a critical maximum, the females would ultimately benefit through their male offsprings' superior ability to recruit a harem (Weatherhead and Robertson, in press). The purpose of the present study was to determine to what extent territorial males differ in their behavior towards females and to establish whether or not such differences reflect success at recruiting females independent of territory quality. We previously reported (Weatherhead and Robertson 1977) that female reproductive success was negatively correlated with the density of females within male territories and positively correlated with territory quality with respect to nest site suitability. We predicted, therefore, that if territory quality could be held relatively constant then the density of females in a male's territory would be an indication of his recruitment ability. This technique is useful in that it allows one to compare recruitment ability relative to territory size. It is also necessary if one is to be able to distinguish between behavioral characteristics related to recruitment and those related to territory acquisition.

METHODS

The area chosen for this study was Cow Island Marsh located near the Queen's University Biology Station, 40 km north of Kingston, Ontario. The vegetation of the marsh is predominantly cattail (*Typha latifolia*), bordered by sweet gale (*Myrica gale*) and alder (*Alnus rugosa*). The marsh is approximately 1 ha in area.

In order to quantify differences between males, behavioral tests were conducted from the onset of breeding in early May until nesting terminated in late June. Tests were performed between 0900 and 1130 two days a week. A single test consisted of a 5 min presentation of a normally postured, freeze-dried female Red-winged Blackbird to a territorial male. The model was attached to the top of a wooden pole positioned so the model was just above the vegetation, close to the center of a territory to ensure that the behavior recorded was that of the territory holder. To avoid behavior associated with nest defense the model was never placed within 5 m of an active nest.

The observer was positioned outside the territory in which the test was conducted, using a portable burlap blind for concealment early in the season and relying on the new growth of vegetation when it became available. The events of the trial were recorded on a portable tape recorder. No male was tested more than once on any given day and the order in which males were tested was varied each day.

The scoring system used was similar to that used by Robertson and Norman (1976) in ranking host aggression to cowbirds (*Molothrus ater*). It was first necessary to rank the behavioral acts in order of increasing intensity of courtship. The basis for the ranking came primarily from the work of Nero (1956a, b) although some intuitive judgments based on field observations had to be made. Such was the case when a departure from strict ordinal ranking was made in scoring an act thought to be of much higher intensity than the act ranked below it. The list of acts and their respective scores is presented in Table 1. The distinction between close and distant acts is that the latter occur further than 3 m from the model.

TABLE 1

SCORING SYSTEM FOR BEHAVIORAL TRIALS

Score	Act.
1	distant silent observation
2	close silent observation
3	distant observation with "check"
4	close observation with "check"
5	distant display flight (6 sec)
6	distant "song-spread" (3 sec)
7	distant crouch or strutting
8	close display flight (6 sec)
9	close "song-spread" (3 sec)
10	close crouch or strutting
15	aggression to other females*
17	pecking at model
20	attempted copulation

* This was considered a recruitment act since it discouraged aggression toward a potential mate by those females already recruited.

The intensity of courtship is also a function of the length of time various acts were elicited during the 5 min trial. Thus, a duration score was also assigned to acts as follows: 1 for acts elicited for less than 5 sec; 2 for acts lasting between 5 sec and 1 min; 3 for acts lasting between 1 and 3 min; 4 for acts lasting greater than 3 min. For discrete acts which were recorded on the basis of how often they were elicited rather than for how long, their duration score in a trial was the mean time required for that act (given in brackets in Table 1) times the number of elicitations. The score for each test was then computed by multiplying each act score by its duration score and then summing these values.

In addition to the model testing, general reproductive information was collected throughout the breeding season. Twice weekly the marsh was thoroughly searched for new nests while the progress of nests found previously was recorded. Territory boundaries were determined as soon as the males became resident. This was accomplished by observing individual movements, use of song posts, and points of conflict between males. Following the breeding season the marsh was surveyed and mapped and territory areas were computed using a polar planimeter. Harem sizes were then determined from nest records as the maximum number of active nests in a territory at any given time during the breeding season.

RESULTS

Figure 1 is a map of Cow Island Marsh indicating the territorial boundaries of the 11 resident males involved in the study. The range of harem sizes and territory areas (see Table 2) are similar to those found in other Red-wing studies (Holm 1973, Goddard and Board 1967, Case and Hewitt 1963, Orians 1961). We conducted 61 tests, with the number of tests per individual

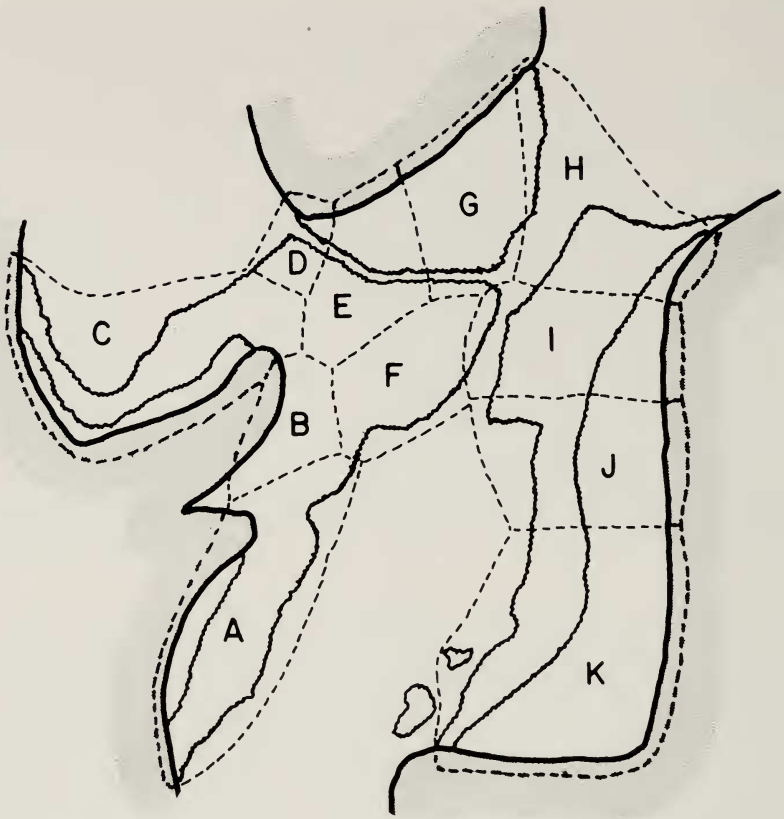

FIG. 1. Territorial males in the study of area. Solid lines indicate dry land (shaded), wavy lines separate cattail from open water and shrub vegetation. Broken lines indicate territory boundaries.

ranging from 4 to 9. Each male was not tested an equal number of times because some males were off their territories on several occasions when they were to be tested. No score was assigned to such trials although a score of zero was given if the male was present at the initiation of a trial and left without eliciting any courtship behavior. Whether such zero scores actually indicated a complete lack of motivation by the male or only a failure to see the model is uncertain. Therefore, the use of such scores in the analysis has been minimized as will be indicated.

Before comparisons could be made between the trial scores of individual males and their respective recruitment success, it was first necessary to test the validity of the scoring system. We felt that if the scores obtained in the

TABLE 2

TERRITORY PARAMETERS AND TEST SCORES FOR ALL MALES TESTED

Male	Territory Area (m^2)	Harem Size	Area Per Female (m^2)	Score Test	Mean Song-Spread Freq.
A	1298	3	433	11.5	4.3
B	213	1	213	20.0	2.7
C	833	4	208	42.4	7.3
D	153	2	77	47.5	10.0
E	475	3	158	20.3	13.0
F	453	3	151	35.5	5.3
G	620	4	155	17.5	2.6
H	1013	4	253	8.0	3.0
I	550	1	550	0.0	2.0
J	863	2	432	13.8	3.8
K	2078	2	1039	4.5	0.7

behavior tests were representative of courtship intensity, then the scores should be highest when the receptive females were most abundant. Nero (1956a) found that female Red-wings are generally receptive around the time of clutch initiation. Thus, by comparing the distribution of dates of clutch initiation with the mean trial score of all males combined over the breeding season, it is possible to determine if the predicted correlation exists. Figure 2 illustrates the results of this comparison. A highly significant correlation (Spearman rank correlation, $r_s = 0.85, p < 0.01$) was found between the abundance of receptive females and the mean test scores over the breeding season. Only non-zero test scores were included.

The results of the model tests for individual males are presented in Table 2. Because of the uncertain meaning of zero test scores, the lowest score was discarded for each male. To prevent any possible biasing due to this dropping of the lowest score, the highest score for each male was also dropped. The mean of the remaining scores was then used to determine the overall test score. If males were able to influence female choice by this behavior, we predicted that those males with the highest overall test scores should also be those that were most successful in recruiting females relative to the qualities of their respective territories. The study area was chosen for its consistent nest site quality and therefore the major differences in overall quality among the territories were due to significant differences in area. Thus, the highest scoring males were predicted to be those with the lowest area per female. Using a Spearman rank correlation, a coefficient of –0.87 ($p < 0.01$) was found for the correlation of female model test score with

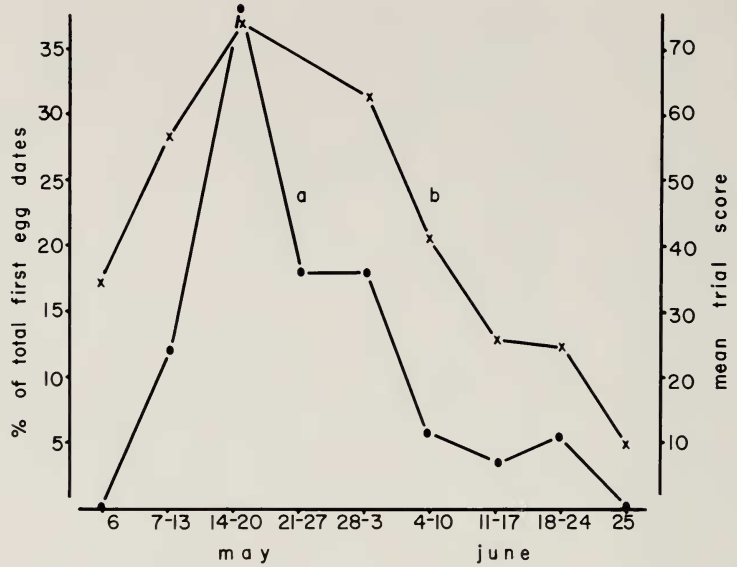

FIG. 2. Distribution of clutch initiation dates (a) and mean trial scores (b) for all males over the breeding season.

area per female. Thus, the males that maintained the highest intensity of courtship to the female model are those that were able to achieve the highest nesting density of females. Since high nesting density is disadvantageous to females, those which chose such a situation must have been influenced to do so by the behavior of the territorial male. Figure 3 clearly demonstrates this finding. As the area per female drops below 300 m^2 the intensity of courtship required by males to increase density further rises sharply.

There is also a significant negative correlation (Spearman rank correlation, $r = -0.65$, $p < 0.05$) between the model test score and territory area (Table 2). This indicates that male behavior associated with recruitment ability is not synonymous with the ability to establish a large territory. In fact, it appears that the 2 are in some way mutually exclusive since the males with the best territories scored the lowest in the behavioral tests.

Of the 13 acts that were recorded in the model tests, the song-spread display was most frequently observed and is perhaps the behavior most commonly associated with male Red-winged Blackbirds. Nero (1956a) considers the song-spread to be a warning display to other males although he does state that it is given more frequently in the presence of females. The mean frequency of song-spread displays per trial where the male was present for the

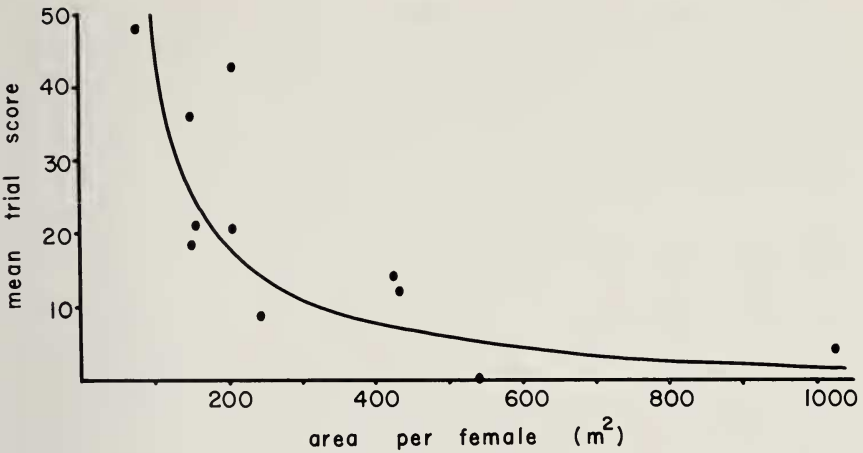

FIG. 3. Individual males' model test scores vs. area per female.

full 5 min was determined for each male. The results of this investigation are included in Table 2. Using Spearman rank correlation, a significant positive correlation ($p < 0.05$) was found between song-spread frequency and mean trial score, and a significant negative correlation ($p < 0.05$) between song-spread frequency and area per female. Thus, it appears that during the time of model testing, this display was of significant importance in female recruitment and did not function solely as a warning display.

DISCUSSION

The notion that males are able to influence the choice of mates by females is not a new one. In his treatment of the topic of sexual selection, Darwin (1871) considered this ability of males to be a major driving force in the evolution of secondary sexual characteristics. The importance of individual differences between males has not been ignored in the Orians-Verner model of polygyny. However, in defining the polygyny threshold in terms of territory quality, the assumption has been made that the difference in qualities of males is reflected in the difference in the qualities of their respective territories. This assumption has not allowed for the possibility that the ability to maintain a good quality territory may be derived from attributes unrelated to those involved in female recruitment. The results of this study suggest that this is in fact the case since recruitment success, as measured by female density, was generally higher for those males with the smaller territories.

Results of other studies of the Red-winged Blackbird support the conclu-

sions drawn above. Smith (1972) investigated the role of the male's red epaulets and found them to be important in territory maintenance but not female recruitment. This indicated that if males were actively recruiting females the epaulets are not important. However, it did not, as Smith suggests, prove that males exert no influence over female choice. Peek (1972) performed similar experiments to those of Smith in which male epaulets were blackened. His results supported Smith's in that the loss of red epaulets resulted in a reduced ability to maintain a territory. However, Peek also performed experiments in which male Red-wings were muted and his results suggest that muted males were unable to obtain mates. In a study of 97 territorial male Red-wings, Weatherhead (1976) reported that only one male remained unmated. This male was also unique in its inability to perform the normal vocalization accompanying the song-spread display, uttering only a high-pitched squeak in its place. The results of the studies cited above suggest that the ability to maintain a territory is related more to visually directed displays while the ability to recruit females has its basis in vocalizations. However, a more recent study by Smith (1976) produced contradictory results. Males that were vocally altered (= muting by Peek) did not appear to suffer any loss of ability to maintain a territory or attract females. Smith interprets the contradictory results as a possible consequence of habitat differences where the 2 studies were conducted. He suggests that only in the best habitats where competition between males is most intense would a male perform poorly if his vocal or visual displays were altered.

It has been demonstrated that males differ behaviorally and that these differences affect recruitment success. However, what remains to be explained is why those males most successful at recruitment are least successful at the establishment of good quality territories. A possible explanation might be that, given a fixed amount of energy available for reproduction there are 2 strategies available. One would be to expend a great deal of energy in establishing a large, good quality territory. In addition to the high energetic costs of the acquisition of such a territory would be the accompanying high maintenance costs throughout the breeding season. This would leave only limited time and energy available for recruitment. The consequence of this strategy would be that fewer females would nest in the territory than would be expected, but because of low nesting density, individual success should be high.

The alternative strategy would be to use very little energy in territory establishment, thereby securing a small territory with low maintenance costs. This would allow much more energy to be devoted to attracting females. The consequence here would be that more females would nest in the territory than would be predicted from its quality. Although female success would be

reduced, the male would still benefit by virtue of the number of females recruited.

As a consequence of the 2 male strategies, females could choose either a high quality territory with low female density and therefore higher chances of nest success or a low quality, high density territory in which the chances of success were reduced but any male offspring produced would be expected to have superior ability to recruit mates.

It is not expected that only 2 "pure" strategies would be observed in nature since males should differ with respect to their total energy available for reproduction. Differences in past experience may also affect how effectively this energy is partitioned. The consequence therefore would be that a range of males might exist such that the most fit obtained many females and high quality territories while the least fit obtained few females and poor quality territories. Between the 2 extremes would be a range of combinations of harem sizes and territory qualities. This would account for the consistent finding of many Red-winged Blackbird studies that harem size and territory area are not correlated (Holm 1973, Case and Hewitt 1963, Orians 1961, Nero 1956b).

SUMMARY

Behavioral tests using freeze-dried female Red-winged Blackbird models were conducted on 11 territorial males through one breeding season. The intensity of courtship in the tests reflected recruitment success but not territory quality, indicating that those male attributes associated with territory establishment differ from those related to female recruitment. A negative correlation was found between recruitment success and territory quality and a possible explanation is presented.

ACKNOWLEDGMENTS

For her assistance with all aspects of the field work we are grateful to K. Clark. We wish to thank R. Norman and F. Phelan for their help in surveying the study area. For their valuable comments, criticisms, and discussion we thank the ecology group at Queen's, and in particular P. Colgan for reading the manuscript. The use of facilities at the Queen's University Biology Station greatly aided this study.

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